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Contrasting vegetation states do not diverge in soil organic matter storage: evidence from historical sites in tundra

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Abstract. Ecosystems where severe disturbance has induced permanent shifts in vegetation and soil processes may represent alternative stable states. To date, little is known on how long-lasting changes in soil processes are following such disturbances, and how the changes in plant and soil processes between the alternative states eventually manifest themselves in soil organic matter (SOM) storage. Here, we analyzed plant density, the shrub : forb ratio, microbial respiration, extracellular enzyme activities and SOM stocks in soils of subarctic tundra and historical milking grounds, where reindeer herding induced a vegetation transition from deciduous shrubs to graminoids several centuries earlier but were abandoned a century ago. This provides the possibility to compare sites with similar topography, but highly contrasting vegetation for centuries. We found that enzymatic activities and N:P stoichiometry differed between control and disturbed sites, confirming that culturally induced vegetation shifts exert lasting impacts on tundra soil processes. Transition zones, where shrubs had encroached into the historical milking grounds during the past 50 yr, indicated that microbial activities for N and P acquisition changed more rapidly along a vegetation shift than those for microbial C acquisition. Although plant and soil processes differed between control and disturbed sites, we found no effect of historical vegetation transition on SOM stock. Across the study sites, soil SOM stocks were correlated with total plant density but not with the shrub : forb ratio. Our finding that SOM stock was insensitive to a centennial difference in plant community composition suggests that, as such, grazing-induced alternative vegetation states might not necessarily differ in SOM sequestration.

Key words: cultural landscape; extracellular enzymes; historical ecology; reindeer; soil carbon stock; tundra.

Introduction

The concept of alternative vegetation states depicts conditions under which a large disturbance induces permanent changes in an ecosystem. According to this theory, ecosystems are resilient to small perturbations but can shift to a different state or equilibrium when the perturbation is severe enough (Beisner et al. 2003). van der Wal (2006) adopted the concept to describe ways and mechanisms by which herbivory modifies the structure and function of tundra ecosystems. Grazing by reindeer in moss- and dwarf-shrub-dominated tundra has been shown to drastically increase graminoid and herb abundance, enhance plant productivity (Olofsson et al. 2001, 2004), and replace lichens with moss-rich ground vegetation (van der Wal et al. 2001, den Herder et al. 2003). It has been hypothesized that grazing-induced vegetation transitions are partially mediated by the fertilization effects of urine and feces (Stark and Väisänen 2014, Barthelemy et al. 2015) and positive feedback of vegetation change on plant litter turnover (Olofsson and Oksanen 2002). Vegetation transitions induced by reindeer do not always follow this pattern (Grellmann 2002, Bråthen et al. 2007, Olofsson et al. 2011, Tømmervik et al. 2012, Bernes et al. 2015). However, many studies have shown that reindeer grazing increases the graminoid abundance in tundra ecosystems (Post and Klein 1996, van der Wal et al. 2004, van der Wal and Brooker 2004, Eskelinen and Oksanen 2006, Gornall et al. 2009, Ylänne et al. 2018).

As humans have always influenced grazer population sizes (Wardle and Bardgett 2004), grazing-induced alternative vegetation states are closely connected with cultural activities shaping the intensity and the spatial distribution of grazing at different time-scales. Historical ecological studies have generally demonstrated a high importance of historical legacies on present-day

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ecosystem structures and processes (Balée 2006, Kardol et al. 2007, Szabó 2015, Valls Fox et al. 2015). This is no less true for high latitudes, although these ecosystems are usually considered to represent natural rather than cultural landscapes (Normand et al. 2017, Egelkraut et al. 2018*a*). The legacy of high grazer densities is not limited to aboveground vegetation but extends to soil microbial activities (Freschet et al. 2014) and nutrient availability (Josefsson et al. 2010, Tømmervik et al. 2010) that may persist in the system long after grazing has ceased. Sites where reindeer herding centuries ago induced a vegetation transition from a shrub- to graminoid-dominated system that is still visible in the present day provide a rare opportunity to study the longevity of the changes in vegetation and soil processes. Since plant species exert an important feedback on soil processes (Hobbie 1992, 2015), we hypothesized that soil microbial respiration and potential enzyme activities at sites with historically but not currently high reindeer densities still closely resemble the rates observed at sites with currently high reindeer densities (Olofsson et al. 2004, Stark and Väisänen 2014).

To date, studies on alternative states in terrestrial systems have largely focused on plant species composition and have provided little empirical evidence on the temporal stability of changes in soil properties and processes. Another question of major importance is how contrasting plant and soil process rates between alternative states (sensu van der Wal 2006) eventually manifest themselves in terms of soil organic matter (SOM) storage. Arctic soils have global significance due to the large C quantity currently stored in these systems (Davidson and Janssens 2006), and herbivores likely have a large impact on this storage (Zimov et al. 2012, Ylänne et al. 2018). Sites with historical vegetation transitions could provide a tool for predicting the impacts of ongoing grazer-induced vegetation transitions on SOM stock because the vegetation transitions at these sites occurred several centuries ago and sufficient time has passed for the slow process of SOM accumulation or loss to be recognizable. According to the present understanding of how plant functional groups drive soil C cycling, a transition from a deciduous shrub to a graminoid-dominated tundra could enhance SOM stock because graminoids produce large quantities of root biomass that are recalcitrant to microbial decomposition (De Deyn et al. 2008, Freschet et al. 2014). The ectomycorrhizal symbionts of typical tundra shrub species may enhance soil C degradation through scavenging organically bound nutrients (Parker et al. 2015) but, through their necromass, also contribute to soil organic matter formation (Fernandez et al. 2016). A study that compared different tundra habitats found that soil C stocks were higher under graminoid-dominated vegetation than those under shrub-dominated vegetation (Sørensen et al. 2018), indicating that the balance of these differing mechanisms could lead to higher soil C sequestration under graminoids.

Here, we analyzed the effects of historical vegetation transitions on plant densities, the shrub : forb ratio, soil properties (moisture, inorganic N, soil organic matter content and stocks) and processes (soil microbial respiration, potential extracellular enzyme activity) using historical milking grounds (hereafter HMGs; Egelkraut et al. 2018*a*) in northernmost Scandinavia that originated from historical Sami reindeer herding. HMGs have a multicentennial history of concentrated reindeer grazing, and although these sites were abandoned a century ago, they are astonishingly stable in terms of both the dominant vegetation and soil nutrient availability (Egelkraut et al. 2018*a*). As predicted for alternative states in tundra (van der Wal 2006), the vegetation in the HMGs is dominated by graminoids and herbs; whereas, deciduous and evergreen shrubs dominate the surrounding tundra (Egelkraut et al. 2018*a*). This allowed us to compare areas with similar underlying abiotic conditions, but contrasting land use and vegetation composition for centuries. We hypothesized that due to an important historical legacy of past land use, soil respiration, and extracellular enzyme activity would be higher in the HMGs than those in the surrounding tundra, and that a multicentennial difference in the dominant vegetation would have led to higher SOM stocks in the HMGs than those in the surrounding tundra.

Materials and Methods

Study area and land use history

This study was conducted in the Padjelanta National Park, northern Sweden (Badjelánnda in the Sami language, 67°19′ N; 16°42′ E) above altitudinal tree line. Between the years 1961 and 2014, average yearly temperatures have changed from −1.8°C to 0.5°C, and average July temperatures increased from 9.7°C to 12°C (SMHI 2016). Average yearly precipitation is 986 mm, of which ~92 mm falls in July. The most common habitat type on nutrient-poor soil is heath dominated by dwarf birch (*Betula nana*), mountain crowberry (*Empetrum nigrum* ssp. *hermaphroditum*), and other evergreen dwarf shrubs and graminoids (e.g., *Vaccinium vitis-idaea*; *Carex* spp.). The most common habitat type on nutrient-rich soils is shrub tundra dominated by willow shrubs *Salix lapponum* and/or *Salix glauca*), tall forbs, and graminoids, e.g., *Geranium sylvaticum* and *Deschampsia caespitosa*). Common vertebrate herbivores include reindeer, rodents (e.g., lemmings and voles) and Ptarmigans with few moose and mountain hare. Reindeer are present as free-roaming groups during June and July with numbers currently in this herding district (Tuorpon, 13,180 km²) between 5,000 and 6,000 (Sametinget 2016). Soils are heterogeneous and dominated by glacial tills and sorted fluvial deposits. The sites are located in a non-permafrost area. As typical for Arctic soils, only weak podzolic profiles are developed, but there are signs of cryogenic activity at many sites.

Reindeer husbandry has been a major means of land use in the area for several centuries. The traditional ways of reindeer herding are well documented in historical records (Olaus 1555, von Linné 1732, von Düben 1873). Contrasting with current practices with relatively free-ranging reindeer, the earlier common form of reindeer herding (AD ~1350–1900 in Padjelanta area; Aronsson 1991) was nomadic and involved tame reindeer herds traveling close to the herders through the mountain landscape during summer (Aronsson 1991, Kamerling et al. 2017). Along their travel route, herders regularly occupied the exact same locations, which were intentionally selected and constructed for the needs of reindeer herding (e.g., loose stones and shrubs cleared away; Aronsson 1991). Herders stayed at each site for a few weeks before moving on to the next ground, gathering the reindeer to the camping site on a daily basis for milking. Owing to this practice, these sites are commonly referred to as "historical milking grounds" (HMGs, Swedish: *mjölkvallar*). Archaeological evidence on human activity (e.g., remnants of fireplaces) corroborates that sites now identified as HMGs truly are those sites used for these activities (Aronsson 2009). The sites were typically located in elevated areas, because this provided a good visibility over the landscape and wind exposure for avoiding mosquitoes (Fig. 1a). The herding activities induced concentrated densities of tame reindeer with associated trampling and nitrogen deposition over many centuries in the same locations. This resulted in distinct and stable patches in the tundra landscape where vegetation transitioned from heath- or shrub-dominated tundra to a plant community dominated by

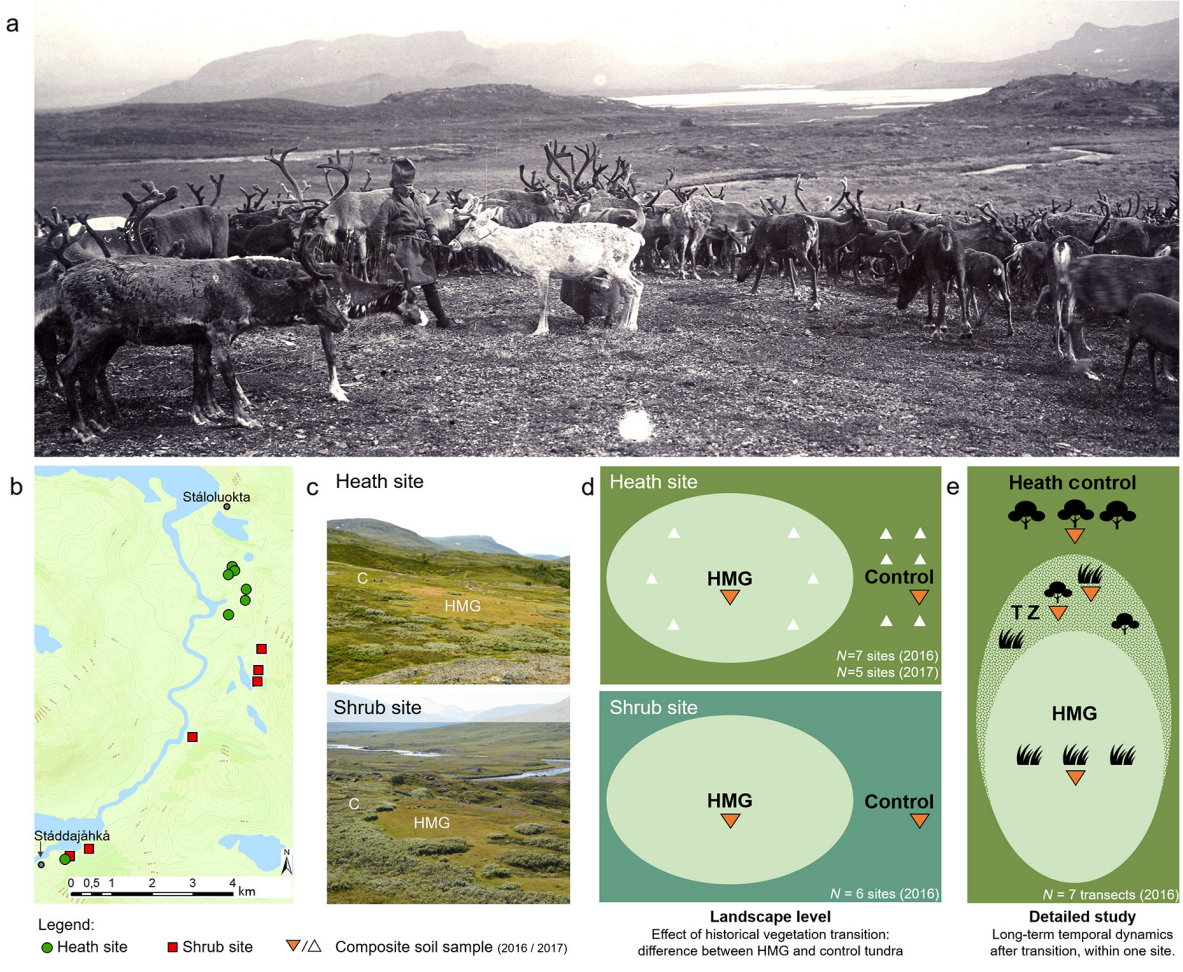

FIG. 1. (a) Sami milking and herding reindeer, northern Sweden, 1902 (photo: Axel Hamberg, Uppsala University library). (b) Overview of the research area including lake Virihaure in the north, and locations of the study sites. Green dots indicate heath sites and red squares indicate shrub sites. (c) Example of a heath and a shrub site, respectively. The letters C (control) and HMG (historical milking ground) indicate the approximate sampling locations (photos: Dagmar Egelkraut). (d) Schematic sampling design for the landscape level study. Sampling in 2016 was done in seven heath and six shrub sites, collecting one composite soil sample at each control and HMG site. Sampling was repeated in five of the heath sites in 2017, but collecting six composite samples per control and HMG. (e) Schematic sampling design for the detailed study in one heath site in (i) HMG, (ii) transition zone (TZ) under graminoid-dominated patch, (iii) TZ under *B. nana* shrub, and in (iv) control, sampled seven times.

herbs and graminoids (Egelkraut et al. 2018*a*). It is noteworthy that herb- and graminoid-rich meadow vegetation is usually not found on high ridges, i.e., in the topographical settings where herders established their camping areas. Soil pH in the HMGs can be as low as 4 and is independent of the vegetation transition (Egelkraut et al. 2018*a*). Major abiotic conditions in the HMGs thus differ drastically from natural meadows that normally are found only in depressions and show a much higher soil pH (a range from 5 to 6.5; e.g., Francini et al. 2014, E. Kaarlejärvi, *unpublished manuscript*). However, similar vegetation transitions are common under high reindeer grazing intensity and are well described in connection with contemporary grazing (Olofsson et al. 2004).

Solid evidence supporting that the vegetation transition in our study sites took place as a result of reindeer herding is also found in pollen records. In Padjelanta, plant species indicating human activity (e.g., *Rumex* sp., otherwise extremely scarce in tundra vegetation; Staland et al. 2010) appear in the tundra vegetation during AD ~1300 to 1400 (Wallin and Aronsson 2012, Andersen 2017). Before that period, pollen analyses only show typical tundra plants demonstrating that a homogeneous tundra landscape was transformed into a mosaic of herb- and graminoid-rich vegetation interspersed with heath- or shrub-dominated tundra. Archaeological evidence suggests that the most intensive use of HMGs likely took place between AD 1600 and 1850/1900 (Aronsson 2009*a*, *b*). By the early 1900s, nomadic reindeer herding practices ceased and transitioned toward free-ranging reindeer, which thus resulted in much lower grazing pressures in the HMGs. Strikingly, the HMGs are still clearly recognizable in the landscape with clear sharp borders from the surrounding tundra, is thus possible to select plots that have experienced a grazing-induced alternative vegetation for several centuries. Whereas the vegetation transition initially was culture-driven, a multitude of mechanisms such as increased soil nutrient availability, high rodent herbivory on shrubs invading the HMGs, and interspecific plant competition partially aided by positive plant–soil feedbacks, jointly explains why these sites are so stable through time (Egelkraut et al. 2018*a*, *b*). At present, reindeer grazing pressure does not appear to differ between surrounding tundra and the HMGs (Egelkraut et al. 2018*a*).

Site selection, vegetation analyses, and experimental design

As HMGs are numerous in our study region, we were able to achieve a robust study design using replicated sites. We selected 13 HMGs in the area between Staloluokta (67°18′ N, 16°42′ E) and Staddajåkkå (67°14′ N, 16°36 E) for this study (Fig. 1b), with an average size of 3,423.9 ± 759.8 m^2 (mean ± SE; Egelkraut et al. 2018*a*). Seven of these milking grounds were located in the heath habitat dominated by *B. nana* and *E. hermaphroditum,* and six were located in the shrub habitat dominated by *Salix* species (Fig. 1c). All HMGs were originally identified during an archeological field survey initiated by the Ájtte Museum (Aronsson and Israelsson 2008). As typical for the location of HMGs in the landscape, they are found on ridges (Fig. 1a, c). In each HMG, we established a 5 × 10 m plot at the center for vegetation analyses. We also selected a paired control plot of the same size outside the HMG area, at a distance of ~50 m on average. We took great care in selecting the control plots for each corresponding HMG at a similar altitude, position in the landscape, aspect, and soil type to reduce the influence of abiotic factors in shaping vegetation and soil properties as much as possible. Although the location of the HMGs in the landscape was based on their functionality for humans (e.g., visibility and mosquito avoidance) and not vegetation, we cannot fully exclude a possibility that there were some minor differences in the initial vegetation between control and HMG sites. However, our well replicated study design should minimize the risk of confounding factors contributing to recorded differences among plot types. Our study area, like all areas of the subarctic European north (Staland et al. 2010), has been influenced by human land use for the last millennia. As such, we do not consider the control plots to represent undisturbed tundra. Yet, the influence of cultural activities involving concentrated reindeer densities extended only to the limited area where people and reindeer resided, beyond which there were no such disturbances. Consequently, the impact of reindeer herding at control sites has been dramatically lower than that in the HMGs. As reindeer grazing induces a vegetation shift toward graminoids only under very high grazing intensities (Bråthen et al. 2007, Bernes et al. 2015), vegetation outside the HMGs remained in a shrub-dominated state (Egelkraut et al. 2018*a*).

To analyze the vegetation composition, we placed a 10-pin point frame (pin diameter 2.5 mm, distance between pins 5.5 cm) in an evenly spaced grid at 40 locations within each 5 × 10 m plot, resulting in 400 points per plot survey at each site (23 July–15 August 2013). Every living leaf or stem touched by a pin was identified to the species level, except for sedges, which were identified to the genus level since intermingling leaves without floral shoots made species determination difficult for all hits. The detailed vegetation data showed that the plant species composition was very similar in all studied HMGs irrespective of the species composition in the surrounding tundra. All HMGs consisted of a diverse graminoid- and forb-dominated community, where graminoids such as *Festuca rubra* and *F. ovina*, *Deschampsia caespitosa*, and *Carex* spp., together with forbs like *Thalictrum alpinum*, *Potentilla crantzii*, and *Rumex acetosa lapponicus* were common species (Egelkraut et al. 2018*a*). Here, we present the shrub : forb ratio and the total plant density, which was calculated as the sum of all hits, to analyze the correlations between the vegetation and soil SOM stocks.

We used the study sites for two different soil sampling campaigns (Fig. 1d, e). First, to analyze the differences in soil properties and processes between control and HMG sites at the landscape level (Fig. 1d), we collected soil samples from 13 sites (n = 7 heath sites, n = 6 shrub sites) on 24 July 2016. Per site, we collected one composite sample of the organic soil layer (entire depth) and a separate composite sample of mineral soil (top 5 cm below the organic layer) at each control and HMG site, respectively. Each composite sample consisted of approximately 20 soil cores (diameter 2.5 cm) spread evenly throughout each plot. To increase the power to detect changes in soil processes in response to historical vegetation transition, sampling was repeated on 11–12 July 2017 in five out of the seven heath sites, but now collecting six composite samples per HMG and control, respectively. These composite samples consisted of five soil cores each.

Second, to analyze the long-term temporal dynamics of soil properties after a vegetation transition, we selected one representative heath site for a detailed study on 24 July 2016 (Fig. 1e). Here, in addition to analyzing the control heath site and the HMG, we utilized the "transition zones" along the edges of the HMGs, where a previous study found slow encroachment due to vegetative ingrowth of border shrubs during the last 50 yr. The encroachment was quantified and mapped in detail using comparisons of high-resolution aerial photos of the sites in 1964 vs. 2008 (Egelkraut et al. 2018*a*). The transition zones form a mosaic of graminoid-dominated patches similar to the HMG vegetation, and heath patches similar to the heath tundra vegetation (Egelkraut et al. 2018*a*). Here, we collected composite samples of organic soil and of mineral soil in (1) HMG, (2) transition zone (TZ) in a graminoid-dominated patch, (3) TZ under *B. nana* shrubs, and in (4) control. Each composite sample consisted of five soil cores (diameter 2.5 cm). This design was replicated seven times in the same site.

Soil analyses

We measured the depth of the organic soil layer from each soil core. Samples were kept cool at the ambient soil temperature (~10°C) until transported to the laboratory (2–3 d). Organic and mineral soil samples were sieved through a 2 mm sieve and analyzed for moisture content (12 h, 105°C) and organic matter content (OMC [%], loss on ignition, 475°C, 4 h). We calculated bulk density (g dry soil/dm^3) using the total volume and mass of samples. We also analyzed water-holding capacity (indicative of mineral soil grain size that regulates soil moisture regimes; mL H_2O/mL soil) by soaking the soil samples in water in closed funnels (2 h) followed by draining (2 h) and measuring the volume of water held in each soil sample (Priha et al. 1999). We also obtained composite samples of root biomass from the soil material that did not pass through the sieve and analyzed root dry mass per area (48 h, 60°C).

The organic layer samples were further analyzed for N concentrations, soil extracellular enzyme activities and soil respiration to depict changes in soil processes in response to historical vegetation transition. For analyzing inorganic N concentrations, a subsample of ~3 g of soil was extracted with 50 mL of 0.5 mol/L K_2SO_4, and the concentrations of NH_4-N (SFS-EN ISO 11732:2005) and NO_3-N (SFS-EN ISO 13395:1997) were determined from the soil extracts using FIAStar 5000 Flow Injection Analyzer (Foss-Tecator, Högnes, Sweden). Extracellular enzyme activities (EEAs) were measured after incubations with selected substrates using a microplate method (Allison et al. 2008). Potential EEAs measured in optimal substrate conditions provide a metric for detecting differences in the production rate of extracellular enzymes by the microbial community (Allison et al. 2007). EEAs can be categorized based on whether they catalyze the degradation of organic compounds that contain only carbon (e.g., β-glucosidase; BG) or compounds that contain both carbon and nutrients (e.g., *N*-acetyl-glucosaminidase, NAG; acid-phosphatase, AP; Sinsabaugh et al. 2008). This separation is not absolute, as N-containing compounds can be used as either a C or a N source, and pH, temperature and substrate availability are important determinants for EEAs (Wallenstein et al. 2009, Hernandez and Hobbie 2010, Kielak et al. 2013). We conducted the incubations at 9°C to correspond to the soil temperatures in the field (12.0°C in the heath habitat, and 9.8°C in the shrub habitat) and adjusted the sodium acetate buffer to mimic the pH in the field (pH 4.4 for heath habitat samples, pH 4.9 for shrub habitat samples). The following substrates were used: paranitrophenyl (pNP)-β-glucopyranoside for BG, pNP-β-N-acetylglucosaminidase for NAG, and pNP-phosphate for AP. BG releases glucose from cellulose, NAG hydrolyzes N-acetyl glucosamine residues from chitin-derived oligomers, and AP catalyzes the release of phosphate by hydrolyzing the phosphoric ester bonds of phosphate groups in organic compounds (Sinsabaugh et al. 2008). The absorbances were analyzed after incubations at 410 nm using a Multiscan FC microplate reader (Thermo Scientific, Vantaa, Finland). Extinction coefficients for calculating EEAs were obtained based on standard curves for paranitrophenol. We analyzed soil microbial respiration from samples taken in the landscape-level study. Subsamples of ~3 g of soil were weighed into 120-mL glass vials after 2–3 days from sieving and incubated at field moisture at 9°C (i.e., close to field temperatures). After a 48-h preincubation, the CO_2 concentrations in the headspace were analyzed every second week for 12 weeks using a gas chromatograph (HP 6890, Agilent Technologies, Wilmington, DE, USA). Incubation vials were flushed with air six or seven days before each soil respiration measurement.

Statistical analyses

The landscape-level data of 2016 were tested using an ANOVA with habitat (heath or shrub tundra) and plot

type (control or HMG) as the fixed factors and site as a random factor. The landscape-level data of 2017 that consisted of only heath sites were tested similarly but with only plot type and site as factors. Data from the heath site used for the detailed study were tested using an ANOVA with plot type as a fixed factor and transect as a random factor. Logarithmic transformations were used when necessary to meet the assumptions of the ANOVA. To examine the correlations between the SOM stocks and other variables, we used a multiple linear regression. To avoid autocorrelation among explanatory variables, linear regression was conducted separately for variables that were correlated with each other, as shown by Pearson's correlation. All statistical tests were conducted using IBM SPSS 22 Statistical Software (IBM, Chicago, IL, USA).

Results

Vegetation, soil properties, and potential enzymatic activities: the landscape-level study

The shrub:forb ratio in the control plots was much higher in the heath habitat than that in the shrub habitat. As the shrub:forb ratio in the heath habitat was close to zero (Fig. 2), no statistical tests on the effect of historical vegetation transition could be conducted.

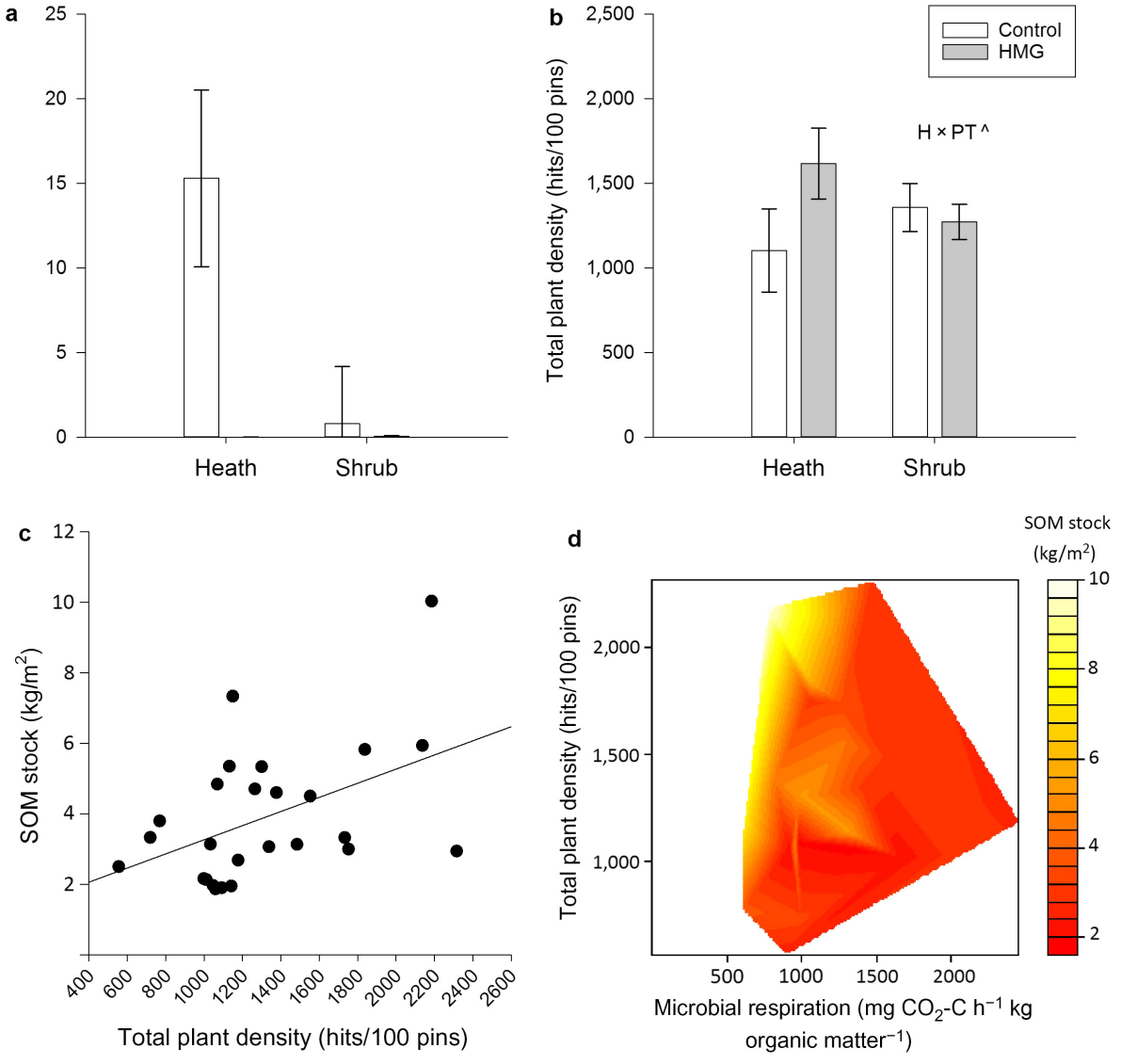

Fig. 2. (a) Shrub-forb–ratio (mean + standard error; S.E.). 2b) the total plant density (mean + S.E.). Hits/100 pins describes the number of living leaves or stems touched by a pin in a 10-pin point frame. H = habitat (heath or shrub habitat), PT = plot type (control or HMG site). ^ = $P < 0.10$. 2c) Correlation between soil organic matter (SOM) stock and the total plant density across 13 study sites at control and HMG sites. 2d) Heat map describing the relationship among soil organic matter stock, the total plant density and soil microbial respiration of CO_2.

TABLE 1. Soil properties and root biomass at control and historical milking ground (HMG) sites in northern Sweden in heath and shrub habitats.

Variable	Heath habitat		Shrub habitat	
	Control	HMG	Control	HMG
Organic horizon				
NH_4-N (mg/kg OM)†,‡	37.5 (22.2)	156.4 (10.2)	139.0 (36.0)	185.1 (11.4)
NO_3-N (mg/kg OM)§	10.8 (7.2)	29.8 (9.8)	6.9 (0.8)	16.5 (2.0)
Organic matter content (%)†	56.2 (3.1)	37.2 (4.3)	41.7 (4.2)	40.5 (4.1)
Moisture%†,§	48.2 (2.8)	42.6 (2.9)	52.5 (2.4)	53.2 (2.9)
Water-holding capacity (mL H_2O/mL soil)†,§	0.72 (0.06)	0.84 (0.04)	0.90 (0.04)	0.98 (0.04)
Bulk density (g dry soil/dm^3)	380.4 (64.4)	479.2 (53.0)	402.8 (44.3)	465.3 (74.1)
Mineral soil				
Organic matter content (%)¶	10.9 (1.6)	8.9 (1.0)	6.7 (1.2)	6.3 (1.0)
Moisture (%)	22.6 (2.0)	22.7 (1.8)	21.8 (2.6)	21.4 (2.2)
Water-holding capacity (mL H_2O/mL soil)†	0.82 (0.02)	0.84 (0.08)	0.70 (0.06)	0.74 (0.06)
Root biomass (kg/m^2)	1.5 (0.2)	1.9 (0.4)	1.7 (0.2)	1.9 (0.2)

Notes: Values are means, with standard errors in parentheses ($n = 7$ for heath; $n = 6$ for shrub habitats).
† Higher in shrub than heath habitat.
‡ Effect of HMG higher in heath than shrub habitat.
§ Higher at HMG than control sites.
¶ Lower at HMG than control sites.

There was no significant effect of historical vegetation transition on the total plant density albeit it tended to be higher at HMG than control sites in the heath habitat (Fig. 2, habitat × plot type–interaction; $P = 0.084$; Appendix S1: Table S1). There were no effects of habitat or historical vegetation transition on the root biomass (Table 1; Appendix S1: Table S1).

In the heath habitat, where the initial NH_4-N pool was lower, NH_4-N pools were >400% higher at HMG than control sites. The effect of historical vegetation transition on the NH_4-N pool was not as strong in the shrub habitat as it was in the heath habitat, and the NH_4-N pool was ~30% higher at HMG than control sites (Tables 1, 2, significant main effects of habitat and plot type, habitat × plot type–interaction). The NO_3-N pools were significantly higher at HMG than control sites irrespective of the habitat type (Table 1; Appendix S1: Table S1). The effects of habitat and historical vegetation transition on soil properties varied between the organic and mineral layers. In the soil organic layer, OMC was significantly lower at HMG than control sites (Table 1; Appendix S1: Table S1). The soil moisture and water holding capacity (WHC) were higher in the shrub than those in the heath habitat, and the WHC was significantly higher at HMG than control sites. There was no difference in bulk density in response to habitat or historical vegetation transition. Confirming that the HMGs and controls did not differ with respect to the underlying mineral soil, OMC and WHC in the mineral soil layer did not differ between HMG and control sites, albeit both were higher in the heath habitat than those in the shrub habitat (Table 1; Appendix S1: Table S1).

There were no significant effects of historical vegetation transitions on BG and NAG activities in the 2016 data (Fig. 3, Table 1). In the 2017 data, BG activity at the heath sites was significantly higher at control than HMG sites (Table 2). AP activity showed an opposite

TABLE 2. Soil inorganic nitrogen pools (mg/kg OM), potential extracellular enzyme activities ($\mu mol \cdot h^{-1} \cdot g^{-1}$ OM), and microbial respiration (mg CO_2-$C \cdot h^{-1} \cdot g^{-1}$ OM) at control and HMG sites in northern Sweden in 2017 (number of sites = 5, replicates per control/HMG = 6).

Variable	Control	HMG	F	P
NH_4-N†	15.6 (2.1)	201.3 (15.4)	544.4	*<0.001*
NO_3-N†	2.3 (0.3)	47.1 (9.0)	199.5	*<0.001*
β-glucosidase (BG)	7.1 (0.3)	5.7 (0.2)	16.6	*<0.001*
N-acetyl-glucosamidase (NAG)	2.3 (0.2)	2.0 (0.1)	2.3	0.134
Acid-phosphatase (AP)	14.5 (0.8)	28.0 (0.8)	221.7	*<0.001*
Microbial respiration	5.9 (0.5)	5.0 (0.2)	3.6	0.064
Organic matter content (%)	38.6 (3.3)	24.1 (1.8)	29.9	*<0.001*
Moisture (%)	46.8 (2.5)	41.9 (1.7)	4.6	*0.037*

Notes: Values are means and SE in parentheses. Data were tested using ANOVA with site as a random factor. Significant effects ($P < 0.05$) are highlighted in italic type.
† Logarithmic transformations were used to meet the assumptions of ANOVA.
Hypothesis d.f. = 1; Error d.f. = 54.

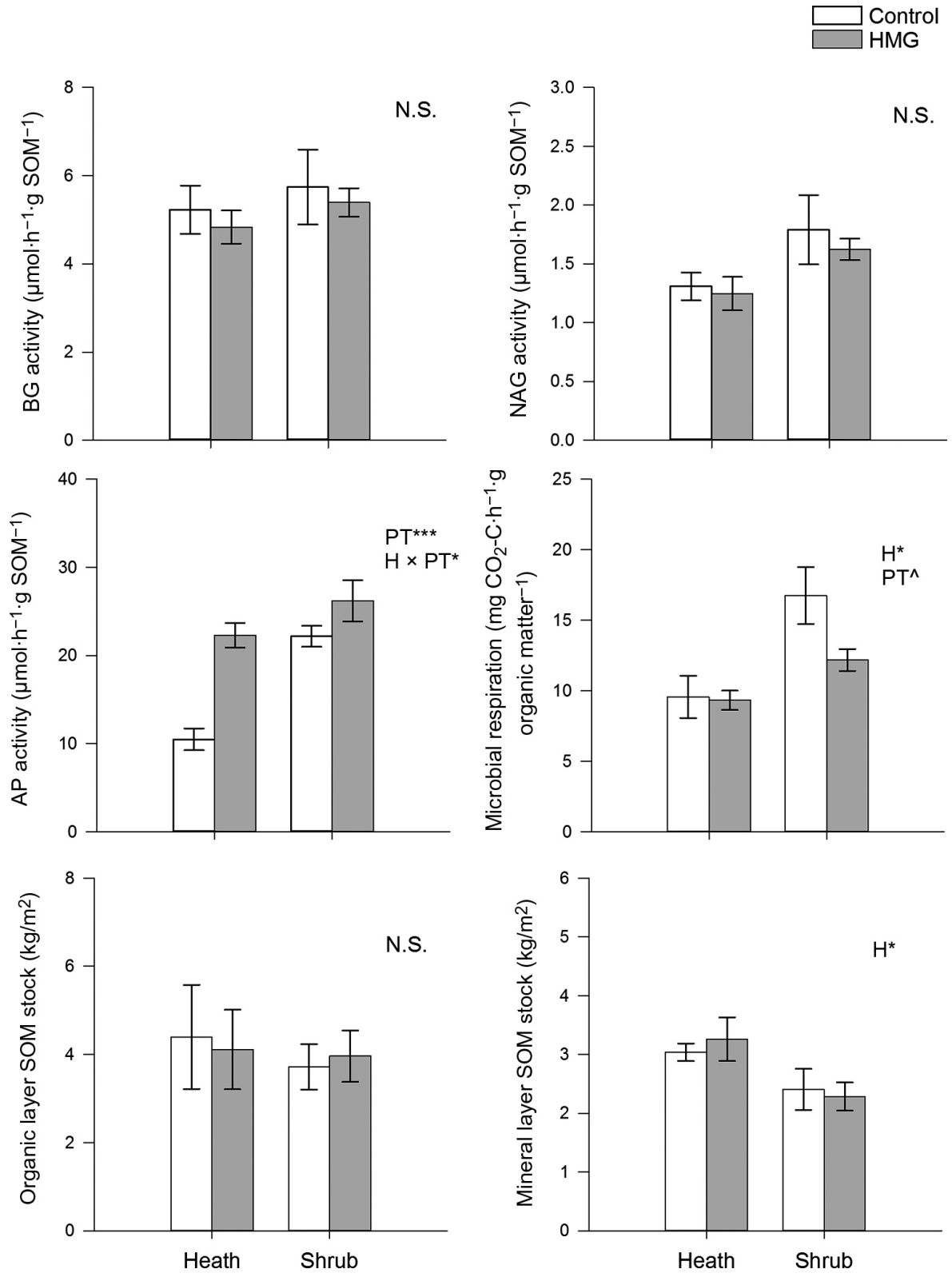

FIG. 3. Extracellular enzyme activities, soil respiration, and organic matter stocks at control and HMG sites in heath (N = 7) and shrub habitats (N = 6; mean ± S.E.). BG: β-glucosidase; NAG: N-acetyl-glucosaminidase: AP: acid-phosphatase. H = habitat (heath or shrub habitat), PT = plot type (control or HMG site). N.S.: non-significant, ^ = $P < 0.10$: * = $P < 0.05$; *** = $P < 0.001$.

pattern and was substantially higher at HMG sites in both 2016 and 2017, and the difference was particularly strong in the heath habitat (Fig. 3, Table 1; significant main effects of habitat and plot type, habitat × plot type–interaction; Table 2). Soil microbial respiration tended to be higher at control than HMG sites in both 2016 (Fig. 3, Appendix S1: Table S1, $P = 0.089$) and 2017 (Table 2, $P = 0.064$). There was no effect of historical vegetation transition on SOM stocks, either when calculated separately for organic and mineral soil layers, or when combined (Table 2; Fig. 3).

The stepwise linear regression showed a significant correlation between SOM stock and the total plant density and microbial respiration. The total plant density alone explained 19.8% of the variation ($P = 0.030$; Fig. 2), and the total plant density and microbial respiration together explained 38.7% of the variation ($P = 0.006$). No relationship between the SOM stock was detected for any of the EEAs, the shrub : forb ratio, or any other soil property, including soil moisture. A heat map demonstrated that the SOM stock increased with the total plant density at sites with low microbial respiration, while there was no relationship at sites with high respiration (Fig. 2).

Soil properties and potential enzymatic activities along a temporal vegetation transition: a detailed study

BG and NAG activities were drastically higher in the heath tundra than those in the HMG, whereas the opposite was true for AP activity (Fig. 4). For BG activity, heath- and graminoid-dominated vegetation patches in the transition zone showed the same activity as found in the HMG (Fig. 4). By contrast, the EEAs for microbial N and P acquisition resembled their vegetation counterparts in the HMG *vs.* heath tundra: NAG activities under heath patches were significantly lower than those in the heath tundra, whereas under graminoid patches, NAG activity was the same as that in the HMG. AP activities were the highest under graminoid-dominated patches in the transition zone. There was no effect on SOM stock in the organic layer; however, SOM stock in the mineral layer, as well as the total SOM stock, was lower under graminoid patches than that in the heath tundra. Soil moisture and OMC% in the transition zones were close to those observed in the HMG (values and test results not shown).

Discussion

Consistent with our hypothesis, grazing-induced vegetation transitions exerted lasting impacts on the soil enzymatic activities, even after the use of the areas had long ended, supporting a strong historical legacy on the soil processes at high latitudes (Freschet et al. 2014, Egelkraut et al. 2018*a*). Enzymatic activities along the transition zone (i.e., area that had been returning to the original vegetation state since the 1960s) revealed that activities involved in N and P cycling were more sensitive to the present vegetation patch than those involved in C cycling. Contrasting with the predictions, we found no difference in the SOM stock in response to centuries of contrasting vegetation. Although the HMGs and controls could be regarded as representatives of alternative states (sensu van der Wal 2006, Egelkraut et al. 2018*a*), the differences in plant and soil processes between them seem to have counteracted each other, leading to no change in soil carbon storage capacity even at multicentennial timescales.

Uncoupled shifts in time in the microbial element acquisition

The EEAs revealed dissimilarities in the historical legacies on soil processes with respect to both the habitat type and whether the enzymatic activity involved soil C, N, or P cycling. Historical vegetation transitions were reflected in the BG and NAG activities in only the heath habitat in 2017. The potential activity of AP, however, was higher at HMG than control sites in both habitats. Tundra soil microorganisms increase the production of a specific enzyme under the demand of the required resource (Weintraub and Schimel 2005*a*, *b*, Wallenstein et al. 2009). The high soil N availability in the HMGs thus likely induced a relative limitation of phosphorus for soil microorganisms, which was counteracted by increased synthesis of AP for P acquisition (Sinsabaugh et al. 2008). These data support the high importance of stoichiometric nutrient requirements for EEAs (Sinsabaugh et al. 2008, Wallenstein et al. 2009, Sinsabaugh and Follstad-Shah 2012, Sistla et al. 2014, Stark et al. 2014), but are the first to show this relationship in a historical ecological context (sensu Balée 2006, Szabó 2015). Supporting that soil microbial processes under historical and existing reindeer densities could be highly similar, the enhanced P limitation in the HMGs agreed with the findings from similar vegetation transition studies with existing high reindeer densities (Stark and Väisänen 2014, Sitters et al. 2017).

The transition zones, where shrubs had slowly encroached into the HMGs after the active use ceased, provided further insight into the soil legacies by showing that over a 50-yr timescale, microbial activities for N and P acquisition changed more rapidly along a vegetation shift than those for microbial C acquisition. In these zones composed of patches of both heath and graminoid vegetation, BG activity (i.e., EEA for degrading C-containing organic compounds) under both vegetation patches was the same as that in the HMG, whereas NAG and AP (i.e., EEAs for degrading N- and P-containing organic compounds) closely resembled their vegetation counterparts in the HMG and the heath tundra. The AP activity in the graminoid patches even exceeded that in the HMGs. Based on these findings, we hypothesize that the strength of historical legacies could vary among the different soil processes. Future studies should

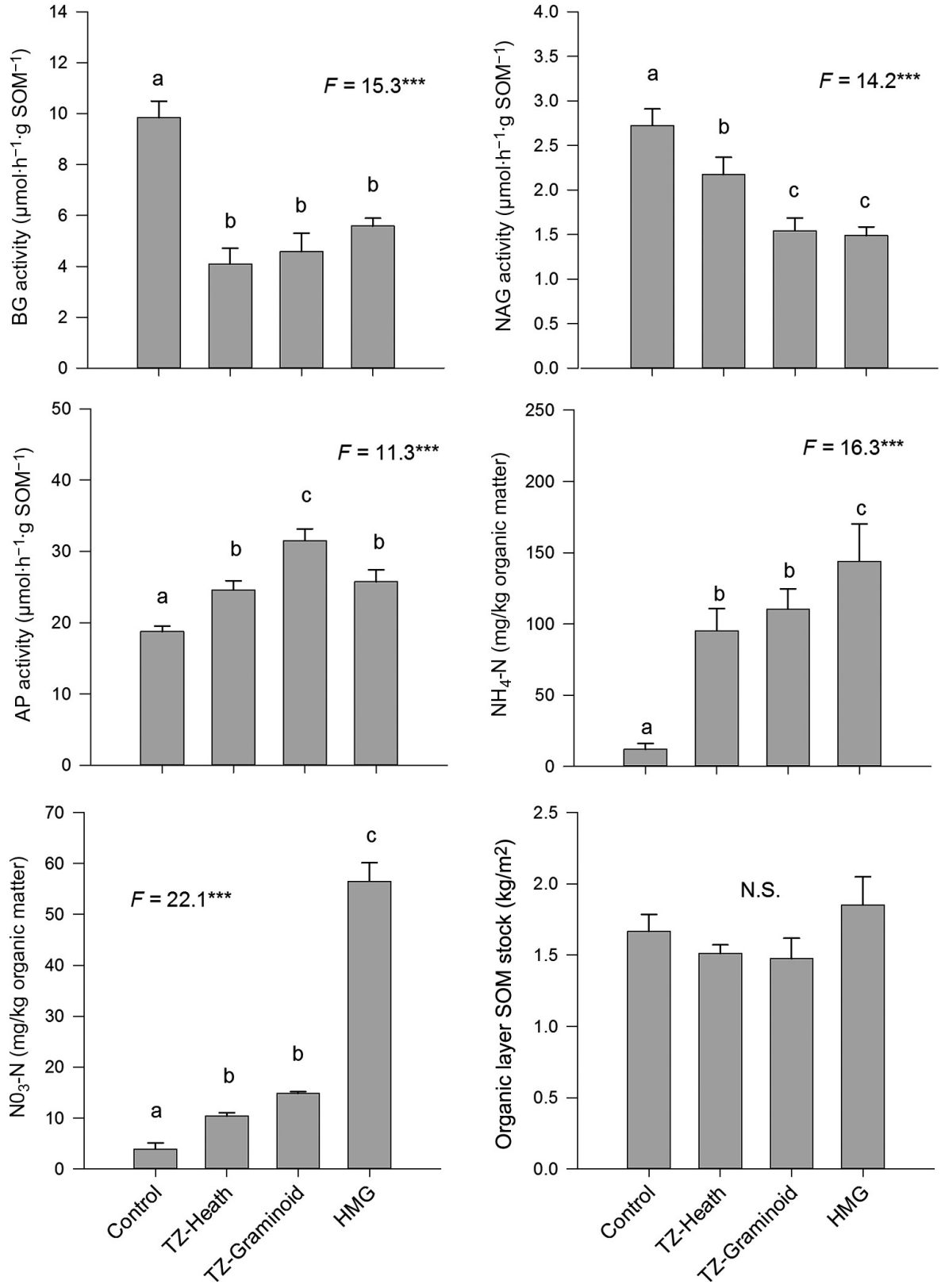

FIG. 4. Extracellular enzyme activities, soil respiration, inorganic nitrogen concentrations, and soil organic matter stock in the organic layer in a selected heath site. The plot types are as follows: heath tundra, heath-dominated patches along the transition

(Fig. 4. *Continued*)

zone (TZ-Heath), graminoid-dominated patches along the transition zone (TZ-Graminoid), and historical milking ground (HMG). Letters indicate significant differences in pairwise comparisons using LSD test following ANOVA; $N = 7$. Values are mean and standard error; S.E. *** $P < 0.001$; N.S., not significant. Hypothesis d.f. = 3, Error d.f. = 16.

consider the possibility that there is a temporal discrepancy in how the microbial potential to degrade C- and nutrient-containing compounds changes through time with vegetation transitions. The borders of the HMGs with a gradually progressing vegetation transition back to the original state indicated that the past rather than the present vegetation governed the microbial potential for soil C degradation, which could obscure the linkages among the present vegetation and soil processes.

Insensitivity of the soil OM stocks to a multicentennial difference in vegetation

It is remarkable that, despite contrasting vegetation for centuries, and a clear legacy of past land use on both vegetation (Egelkraut et al. 2018*a*) and soil processes, we found no difference in SOM stock between HMG and control sites. Several reasons could explain the insensitivity of the SOM stock to a multicentennial ecosystem change. It has been suggested that whether a transition to another vegetation state in response to grazing increases or decreases soil C sequestration could depend on the type of vegetation that is replaced through grazing (Ylänne et al. 2018). Heath- and shrub-dominated tundra with mixed *B. nana* and *E. hermaphroditum* or *Salix* willows store carbon in the woody biomass and produce slowly decomposable litter, but also maintain high rates of C cycling via labile C inputs and ectomycorrhizal symbionts that efficiently degrade soil organic matter (De Deyn et al. 2008, Buckeridge et al. 2010, Parker et al. 2015). A transition of this type of vegetation to a grassland may have ambivalent effects on C degradation as graminoid leaves decompose rapidly (Olofsson and Oksanen 2002), but graminoid roots contain high concentrations of decomposition-resistant aliphatic compounds that often accumulate in soils (Rasse et al. 2005, Hobbie 2015). Simultaneously, the most common mycorrhizal association shifts from ecto- to AM mycorrhiza, which does not directly degrade organic compounds (Xu et al. 2018). Mosses that are highly important to the tundra soil C stocks (Street et al. 2017) also increase in abundance in the HMGs (Egelkraut et al. 2018*a*). As plant functional groups govern soil C sequestration through a diverse suite of mechanisms (De Deyn et al. 2008, Hobbie 2015) and grazing simultaneously alters the relative abundances of several plant functional groups, the effects of the vegetation shift could be hidden by the different changes counteracting each other.

Alternatively, the quantity of plant litter input could outweigh the importance of plant community composition for the SOM stocks. The correlative evidence that indicated an association between the SOM stock and the total plant density across the landscape would support this interpretation. Along with the aboveground plant density, we did not find effects of historical vegetation transition on root biomass, either, and previous studies in tundra have found strong relationships between treatment effects on fine root production and soil C stocks (Sullivan et al. 2007). It is widely acknowledged that the majority of organic carbon in the accumulated soil organic matter is not inherently slowly degradable by soil microorganisms either generally (Marschner 2008, Kleber 2010, Prescott 2010, Kleber et al. 2011) or in tundra (Sjögersten et al. 2003, Vancampenhout et al. 2009). Rather than chemical "recalcitrance," the transformation of plant-derived compounds into microbial residues, the soil microbial potential for synthesizing extracellular enzymes to catalyze organic matter degradation and soil moisture could constitute key factors regulating soil C sequestration (Schimel and Weintraub 2003, Allison 2006, Kleber 2010, Schmidt et al. 2011). If environmental conditions governing plant litter input and C decomposition across the landscape constitute a more important driver of SOM sequestration than the plant community composition, it would explain why the SOM stock was insensitive to a centennial difference in the plant community composition.

While our findings on SOM stocks in historical sites contrasted those from different natural tundra habitats, they were consistent with the findings from sites with existing grazing. A study that compared natural tundra habitats have found that SOM stocks were higher under graminoid-dominated vegetation than those under shrub-dominated vegetation, indicating lower soil C sequestration under shrubs than that under graminoids (Sørensen et al. 2018). Differences among natural habitats, however, integrate several site properties, such as vegetation, topography, exposition, and underlying bedrock, and show their combined impact on soil C sequestration (Campioli et al. 2009, Parker et al. 2015, Sørensen et al. 2018). Here, we compared the SOM stocks in sites with culturally induced historical vegetation transitions, and in our experimental design, environmental factors such as topography, exposition and soil pH between control and HMG sites were the same. We can thus attribute the differences directly to changes in vegetation composition. Similar to our present findings, reindeer exclosure experiments in boreal forests (Stark et al. 2000, 30 yr; Köster et al. 2015, 50 yr; Köster et al. 2013, 100 yr), the forest–tundra ecotone (Stark et al. 2007, 15 yr), and subarctic tundra (Ylänne et al. 2018, 50 yr) have found equal soil C or SOM stocks under divergent grazing intensities despite changes in vegetation. One subarctic tundra site showed enhanced soil and ecosystem C stocks after a vegetation

transition from *B. nana* to a graminoid tundra (50 yr, Ylänne et al. 2018). The insensitivity of the soil C stock to grazer-induced vegetation transitions seems to form a general pattern across several temporal scales and vegetation responses to grazing, providing evidence that environmental conditions could indeed be a more important driver of soil C sequestration than the grazer-induced effects on plant species composition and biomass.

The "carbon-neutral" effect of reindeer grazing in northern ecosystems (Köster et al. 2015) provides a novel angle for understanding the conditions that would result in different soil C sequestration rates in alternative ecosystem states (sensu Beisner et al. 2003, van der Wal 2006). Based on the present evidence on reindeer grazing, alternative states induced by high herbivore densities might not exhibit different soil C sequestration rates if only biological mechanisms are involved. The situation would be different in cases where grazers induced organic and mineral soil losses that led to a permanent decrease in the ecosystem nutrient stocks (van de Koppel et al. 1997, Normand et al. 2017). It has also been suggested that in Arctic ecosystems, herbivores could protect the large soil C pools stored in permafrost by preventing soil thaw (Zimov et al. 2012) although evidence from tundra suggests that even melting permafrost may lead to a neutral effect on soil C stocks (Sistla et al. 2013). These cases would also fit with the theory of alternative stable states (Bernes et al. 2015). Importantly, some studies have also shown that the soil C stock increased in response to long-term grazing in temperate grasslands (Henry 2009) and subarctic tundra (Ylänne et al. 2018). Rather than assuming a consistently negative effect of grazing on the ecosystem C stock (Tanentzap and Coomes 2012, Normand et al. 2017), future studies should determine the conditions under which alternative states lead to increasing, decreasing, or no effect on ecosystem C sequestration. Sites with demonstrated historical vegetation transitions could provide a powerful tool for testing ecological theories and predictions across long timescales and improving predictions of the long-term consequences of ecosystem change as well as understanding their main drivers.

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